THE CRANIAL NERVES OF *NEOCERATODUS*.

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(Four Text-figures.)

[Read 28th March, 1945.]

Introduction.

Early in 1939 Mr. Heber Longnan, Director of the Queensland Museum, sent me a very perfectly preserved specimen of *Neoceratodus* (*Epiceratodus*). I wished to check again the innervation of certain of the muscles, and for his very prompt reply to my request I thank him very much. It seemed a pity to destroy so fine a specimen for so small an investigation, so I decided to dissect out the roots of the cranial nerves and describe them together with their distribution and their relations to other structures.

Before commencing the description of the nerves I wish to remark on that which I regard as the most interesting result of the work. I was very forcibly struck by the fact that although the brain was very much longer than that of the fishes the anterior end of the medulla was in precisely the same position relative to the otocrane as that of the fishes. It is probable that the presence of the lateral cranial fenestra emphasized this identity of relationship. I then rediscovered an obvious fact, one which, of course, has been known to all anatomists for very many years. The rediscovery was interesting because, although so obvious, it has never, so far as I can ascertain, been categorically stated nor has it been given recognition. The failure to take cognizance of the relation of the medulla to the otocrane has resulted in the misinterpretation of archaic fish skulls by palaeontologists, notably Watson (1925), Säve-Söderbergh (1936), and Westoll (1943).

Although the brain of *Neoceratodus* anteriorly to the medulla is very much longer than in any of the fishes, the hind-brain is, as already stated, in precisely the same position relative to the otocrane as that of the fishes. Room has been made for this elongation in the sphenoidal region of the skull. In the fishes this part of the cranial cavity is occupied by the olfactory peduncles. In the amphibians the sphenoidal part of the cranial cavity is occupied by the elongated fore-brain and olfactory lobes as in *Neoceratodus*. In the Sauria there is a return to the fish condition, only the olfactory peduncles are lodged in the sphenoidal cavity. In the Theria room is made for the expanding brain, and the cavity is terminated abruptly by the lamina cribrosa and there is no sphenoidal cavity. Throughout the Vertebrata the anterior end of the medulla is to be found in very close proximity to the transverse plane of the anterior limit of the otocrane, and of course the pituitary body is always situated just a little farther forward.

All this is almost platitudinous, the facts are so obvious and have been well known for decades. But although that is so, it has not been taken cognizance of and on that account is well worthy of restatement.

A reference to the palaeontological papers referred to will reveal that these investigators have located the fore end of the hind-brain in the anterior part of the sphenoidal cavity and the pituitary body actually in the ethmoidal region. The incongruity of their conclusions has not been realized by them for they have agreed to designate the bone beneath the hypothetical pituitary fossa basisphenoid. We are presented with a basisphenoidal bone divorced by nearly half the total length of the skull from the otocrane, or in the alternative a basisphenoid bone which underlies the whole length of the orbital region.

Description of the Roots and Distribution of the Nerves.

The olfactory peduncles are very short and thick, and, moreover, they expand almost at once so as to embrace the postero-medial one-third of the olfactory capsule (Fig. 1).

This shortness of the peduncles is in marked contrast with fish brains. The forebrain has grown much further forward in the skull than is the case in any of the fishes. Comparing the condition here with that of the fishes, accommodation for the increased size of the brain had been obtained by utilizing and enlarging the sphenoidal

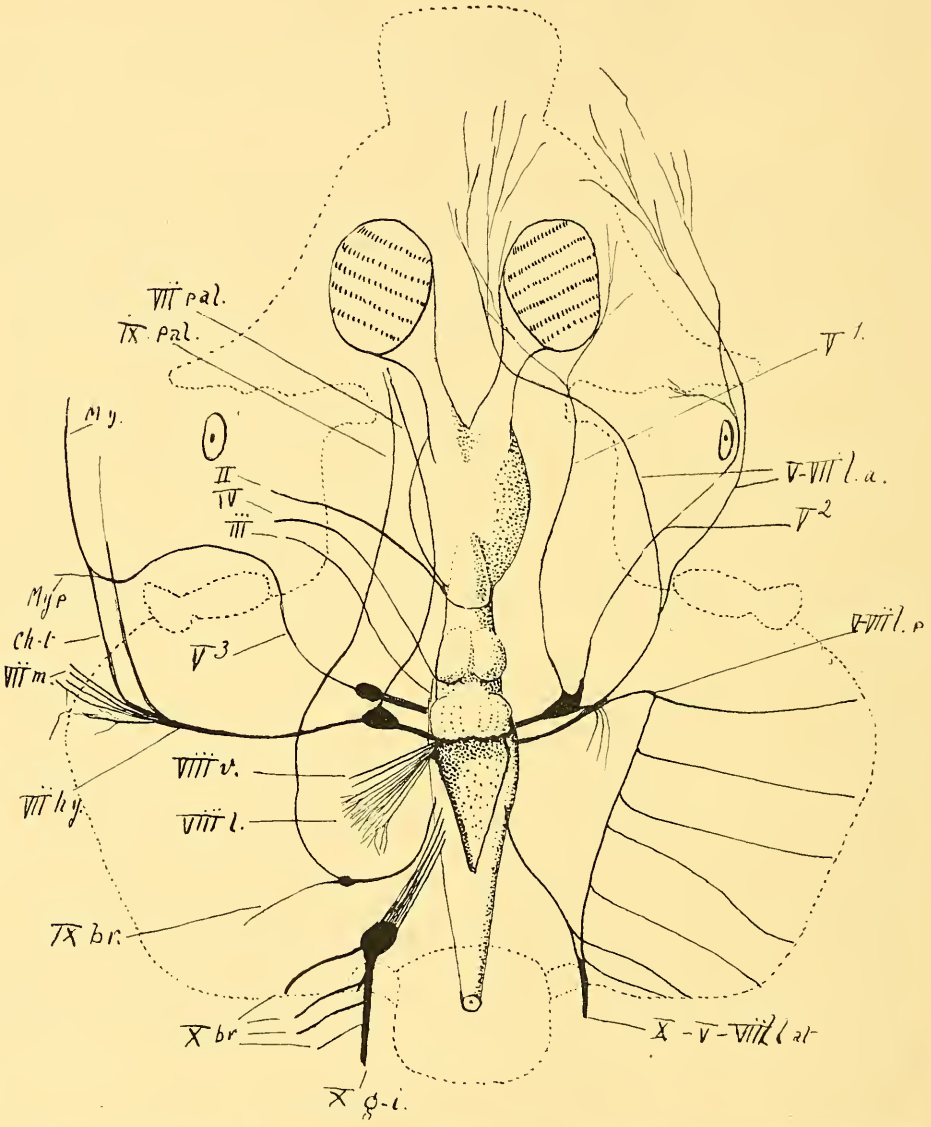

Fig. 1.—*Neoceratodus.* Semi-schematic dorsal view of the distribution of the cranial nerves. Ch.t., chorda tympani. My., anterior myloid nerve. My.p., posterior myloid nerve, the motor nerve to muscle CSV1. II., optic nerve. III., oculomotor nerve. IV., the pathetic nerve. V., ophthalmic division of the fifth nerve. $V.^2$, mandibular division of the fifth nerve. $V.^3$, maxillary division of the fifth nerve. The motor twigs to the muscles of mastication not shown. V-VII l.a., anterior division of the trigemino-facialis lateralis nerve. V-VII l.p., posterior division of the same nerve. VIII hy., hyomandibular division of the facialis nerve. VII m., motor twigs of the facialis nerve to the CS2, interhyoideus and levator hyoidei muscles. VII pal., palatine division of the same. VIII l., labyrinthine division of the eighth nerve. VIII v., vestibular division of the same. IX br., branchial division of the ninth nerve. IX pal., palatine division of the same nerve. X br., branchial branches of the vagus nerve. X g. i., gastro-intestinal division of the same nerve. X-V-VII lat., posterior lateralis nerve.

extension of the cranial cavity which, throughout the fishes, contains only the long, narrow olfactory peduncles. In the fishes, in the great majority of instances, the anterior limit of the brain is located no further forward than the posterior limit of the orbit; in *Neoceratodus* the fore-brain lies medially to the orbit, extending forward almost as far as its anterior boundary. This is not due to a forward shifting of the whole brain, because the pituitary body and the optic chiasma are located in the same position relative to the orbit and to the rest of the skull as it is in the fishes.

Another factor determining the brevity of the olfactory peduncles is that the olfactory capsules have expanded in a caudal direction by the utilization of that cavitation of the ethmoidal mass, which is so constant a feature of the fish skull.

The nasal capsule is remarkably large. Its sensitive mucosa is apparently confined to the roof and a small segment of the posterior wall. It does not appear to be generally appreciated that *Neoceratodus* has no external nostril. The anterior narial apertures are situated on either side of the mid-line within the margin of the upper lip. The lip itself is broadly grooved immediately within its border and this groove leads to the anterior naris on the roof of the mouth. The posterior nares are also located in the roof of the mouth, further back and a little more laterally. There is no partition or other obstruction on the floor of the olfactory capsule between these two apertures; a probe introduced into either may be pushed straight out through the other if it is but kept against the floor with a little pressure to pull that floor downward. Just in front of the angle of the mouth both upper and lower lips are grooved to provide an entrance to a peculiar, laterally compressed cavity (bursa innominata) lined by the oral mucosa. This appears to have been regarded by some, at least, of the recent students of the fossil Crossopterygians as the external naris of the Dipnoi. The cavity in question is not connected with the olfactory capsule at all. It extends dorsally in the side of the mouth and backward until it lies medially to the depth of the anterior boundary of the orbit, and also forward until it lies laterally to the lateral wall of the olfactory capsule. The two cavities together call to mind the single cavity in the ethmoidal region of *Latimeria* (Smith, 1940).

The optic nerves of *Neoceratodus* are rather thinner than might have been expected, and there is nothing of particular interest to record in connection with their course or relation to contiguous structures.

The location of the orbit relative to the skull is, however, of some interest. The eye itself is small (a feature wherein the Dipnoan resembles the rest of the Amphibia rather than the fishes) and has been located far forward in the space between the two main massives of the cranium. The static location of the hinder half of the brain is again emphasized by consideration of the varying location of the eye to the skull. It is placed further back in the generality of the fishes than it is in Dipnoans, and further forward in the rest of the Amphibia than it is in these. The optic chiasma, however, remains in the same relative location and the length of the optic nerve is varied to meet the different distances to the eye.

The Oculomotor Nerve.

The third nerve arises from the base of the brain a short distance caudal to the pituitary body, and, as is usual, by a single root. The point of origin is medial to that longitudinal eminence on the ventrum of the brain which is due to the descending pyramidal fibres. The nerve runs forward and laterally for a short distance across the ventrum of the mid-brain, then laterally through the loose connective spongework* in which the brain is packed within the cranial cavity, to its own canal in the lateral wall.

* The nature of this "packing" tissue is a character which the Dipnoan shares in common with the fishes rather than the rest of the Amphibia. In the Dipnoan the space between the brain and the wall of the cranial cavity is, as in the fishes, quite extensive. It is occupied by fine strands of connective tissue none of which has any tensile strength and all of which are well separated from each other, so that the brain may be said to be lightly suspended in a bath of serous fluid by a multiplicity of fine, weak strands of tissue. Of course it rests upon the floor of the cavity. In the rest of the Amphibia the brain case is more nearly a reasonable "fit" for the brain, the empty space is much less and the packing tissue more plentiful and stronger.

This canal is situated behind and ventral to the optic canal; it runs through the wall diagonally forward and laterally. The nerve emerges on to the outer surface of the skull behind and below the optic nerve but above the ophthalmicus profundus. It crosses this last nerve before it reaches the "wall of the orbit", but has divided into two branches before doing so.

Its distribution to the ocular muscles is without comparative interest.

The Pathetic Nerve.

The fourth nerve arises, by a single root, from the dorsum of the mid-brain half-way between the posterior boundary of the pineal body and the anterior boundary of the cerebellum. It is a larger nerve than might have been anticipated and quite readily found. Its course is parallel to that of the third nerve but further forward and dorsally. It also emerges from the cranium through a foramen of its own. This runs nearly parallel to the optic canal and almost directly above it but just a little behind it. The nerve emerges dorsally to the optic and has but a short course before penetrating the "wall of the orbit",* close to its inner, deep end.

The Trigeminal Nerve.

The fifth nerve arises from the anterior end of the medulla, laterally to both the pyramidal and lateral columns. It was not possible to separate the roots of this nerve; they are so closely bound together that the nerve appears to arise by a single root composed of a number of bundles of strands of fibres. The number of the bundles was quite indeterminate and varied in four cases, apparently with the skill and patience devoted to their separation.

The root passes across the intervening space and enters the prootic foramen before the gasserian ganglion is reached. From the ganglion, the R. ophthalmicus profundus is first given off. This runs directly forward in the thickness of the cranial wall. The early embryonic stages, however, indicate quite clearly that the portion of the wall lateral to the nerve is the processus ascendens quadrati and that the posterior boundary of that structure is the anterior wall of the canal through which the rest of the nerve runs to reach the external aperture of the prootic foramen.

The anterior aperture of the ophthalmicus profundus canal is situated low down on the side wall of the cranium a short distance posterior to the posterior wall of the orbit. As soon as the nerve emerges it splits into smaller superior and larger inferior divisions. The former runs forward and dorsad and divides into two fine terminal branches which pass forward and round the orbit, medially, in the subcutaneous tissues. The inferior division passes forward close to the inferior edge of the skull, it rises slightly so as to pass above the optic and oculomotor nerves and the attachment of the dorsal periphery of the orbital wall to the cranium. The nerve lies against the ascending process of the palatine as it passes dorsad to reach the dorsal surface of the skull just at the lateral end of the fronto-prefrontal suture. In this situation it lies behind the dorsal wall of the olfactory capsule and divides here into four terminal branches. Two of these run forward in a canal lodged in the cartilaginous tectum nasi, but dorso-laterally to the capsule, the other two branches are similarly situated but pass dorso-medially, lying ventrally to the terminal branches of the ophthalmicus superficialis VII. This branch of the fifth nerve appears to carry no lateralis fibres, for none of its twigs was traced to a special cutaneous sense organ or canal.

After giving off the profundus trunk the gasserian ganglion fuses with that of the lateralis trunk of the facialis nerve. The actual exchange of fibres effected by this fusion cannot be determined by dissection, but it appears that fibres from the trigeminalis root pass to the lateralis nerve and that fibres from the lateralis pass into the ramus maxillaris trigemini.

* This term "wall of the orbit" has been used above and it might be well to explain that all the oculomotor muscles and the terminal segments of their nerves, the optic nerve, ophthalmic artery and the eye itself are wrapped about by a loose, but fairly dense and relatively thick sheath of connective tissue which is attached to the deep layers of the skin all round the eye. It is this sheath which is being designated as above.

The whole of the ganglionic mass is lodged within the prootic canal.

From the external aperture of this canal the following nerves emerge, and in the following order from before backwards. The short motor twigs of V3 to the muscles of mastication, the mylohyoid nerve, the ramus maxillaris trigemini, the ramus ophthalmicus superficialis VII and three or four twigs from lateralis VII. The main trunk of the lateralis VII turns caudally at the outer end of the canal and enters the lateralis canal instead of emerging with the other nerves (Fig. 2).

The motor twigs to the muscles of mastication are four in number; they enter the contiguous surfaces of the two great muscle masses very soon after emerging from the canal, two to each muscle.

The rest of the mandibular division of the fifth nerve continues forward in the layer of loose connective tissue which intervenes between the contiguous surfaces of the two muscles. Just posterior to the fusion of the tendons of the muscles, this "myloid" nerve reaches the surface. From here it runs around the combined tendons close to their insertion, first forward, then laterally, and finally caudally until the posterior opening of the myloid canal is reached.

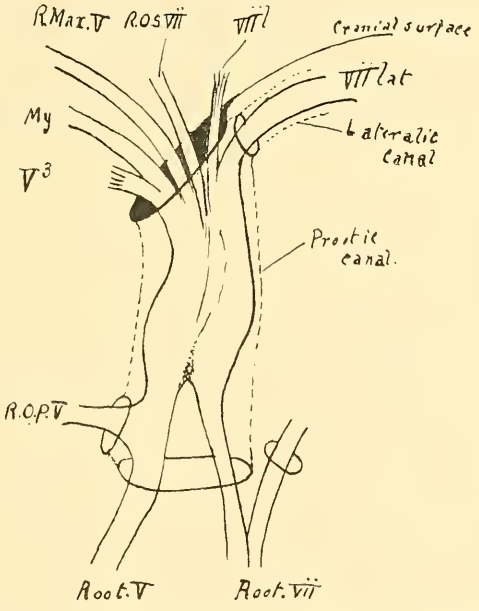

Fig. 2.—*Neoceratodus*. The roots, ganglia and branches of the fifth and seventh nerves. R. max. V., ramus maxillaris of the fifth nerve. R.o.p. V., ramus ophthalmicus profundus of the fifth nerve. R.o.s., ramus ophthalmicus superficialis of the seventh nerve. Other lettering as in Fig. 1.

For a very short distance after entering this canal the direction of the nerve is transversely out from the mid-line and ventrad. It then turns abruptly forward and runs along the full length of the mandible to the posterior limit of the very broad symphasis. At the point where this nerve turns forward it gives off the posterior myloid nerve, which is apparently a purely motor nerve to the M. intermandibularis. As it reaches its termination the nerve gives off a number of small branches.

A very short distance in front of the point where the posterior myloid nerve is given off the main nerve is joined by a communicating branch of the hyomandibular division of the nervus facialis (the interior mandibular nerve) which entered the myloid canal with it but which does not fuse until after the smaller branch has been given off (Fig. 3).

The maxillary division of the trigeminal nerve runs forward between the muscles, above the mandibular division. It emerges from between the muscles and continues

forward until the posterior wall of the orbit is reached. It then runs round the outer side of this and below it and then divides into two branches. The smaller, dorsal branch breaks up into its terminal twigs in the tissues of the lip, and innervates the posterior portion of the innominate pouch. The larger, ventral branch runs right forward and its terminal twigs are distributed to the mucosa of the antero-lateral part of the palate, the mucosa of the lip and that of the anterior portion of the innominate pouch. Though it cannot be stated definitely, it is confidently believed that terminal twigs of both branches of this nerve supply both lateral line and pit organs along the edge of the upper lip nearly to the extreme forward end.

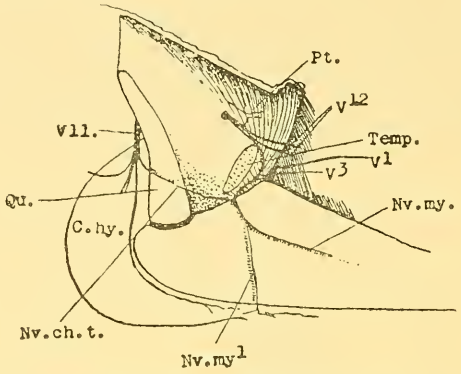

Fig. 3.—*Neoceratodus.* Semi-schematic presentation of some of the branches of the Vth and VIIth nerves. C.hy., Ceratohyoid; Nv. ch-t, Communicating branch of the VIIth to the myloid branch of the Vth; Nv. my., Myloid nerve; Nv. my.^{1}, Posterior myloid nerve; Temp., Tendon of the tempo-masseteric muscle.

The sixth nerve arises from the ventro-lateral surface of the medulla behind the roots of the seventh and eighth nerves, by three small roots. The nerve runs forward below the brain and was unfortunately torn loose so that its course could not be determined.

The Facialis Nerve.

The seventh nerve arises by three, relatively, widely separated roots, the lateralis, combined sensori-motor and otic. The lateralis root arises so high on the side of the anterior end of the medulla that it may be said to arise from the lateral lip of the anterior end of the fourth ventricle. The combined sensori-motor root arises directly ventral to it just above the closely clustered roots of the eighth nerve. These two roots are of very nearly equal size, the otic root is less than half the thickness of these and arises in front of the inferior roots of the eighth nerve. The origin of this root is very close to the labyrinthine roots of that nerve and it passes between the two vestibular rami on its way to join the general sensori-motor root (Fig. 4). Both the larger roots split into larger and smaller divisions, and these smaller divisions each pass to the other root. The otic root joins the general sensori-motor root before that is joined by the lateralis contribution and after it has given off its own contribution to the lateralis. In the result the nervus facialis roots have now been collected into two main trunks, the nervus lateralis dorsally and the facialis proper ventrally.

The fusion of the lateralis ganglion with the gasserian has already been described, and it was noted that three branches of the lateralis nerve branched from the lateralis portion of the ganglion.

The ramus ophthalmicus superficialis VII is probably a mixed general and special, lateralis, cutaneous sensory nerve, and in all probability contains the whole of the fibres received from the sensori-motor root by the lateralis nerve. This nerve divides into anterior and posterior divisions almost before it leaves the ganglion. The posterior division, after a very short course between the muscles of mastication, breaks up at their surface into four to seven separate strands which are distributed to the subcutaneous

tissues between the orbit and the anterior boundary of the fleshy wall of the branchial chamber, but reaching towards the mid-dorsal line and stopping short of the post-orbital lateral line canal, which runs caudally just above the level of the angle of the mouth. The main part of the nerve runs forward superficially to the ramus maxillaris trigemini, gives off several small twigs to the tissues of the skin and lateral line organs immediately behind and below the eye, and passing, in the subcutaneous tissues, medially to the orbit terminates in branches which are distributed to the pit and lateral line organs of the snout, medially to and in front of the location of the olfactory capsules.

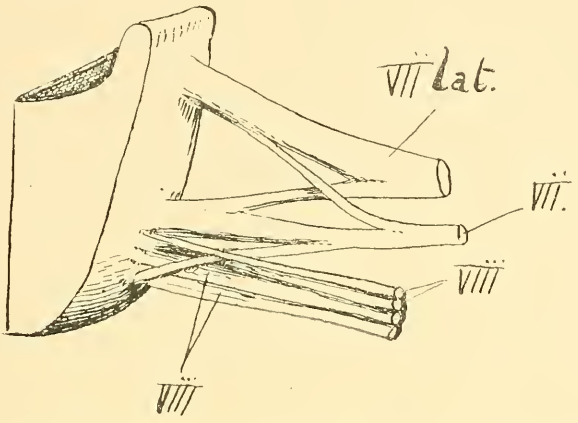

Fig. 4.—*Neoceratodus*. Semi-schematic presentation of the roots of nerves VII and VIII.

The lateralis nerve turns caudally close to the external aperture of the prootic canal and enters the lateralis canal. This is lodged in that extraordinary expansion of the otic root of the quadrate which constitutes the cartilaginous roof of the branchial chamber and which, as Edgeworth (1925) demonstrated, has incorporated into it and completely obliterated, the diminutive hyomandibular cartilage. The course of the canal is curved with the concavity of the curve medially. It runs caudally, dorsally and medially. Whilst within the canal five twigs are given off. Each of these runs in a canal through the cartilage to its lateral edge. In this situation the nerve emerges immediately deep to the lateral line canal and each is distributed to a segment of it. Just before the lateralis VII reaches the posterior aperture of the canal it is crossed superficially by a branch of the lateralis X which runs parallel to the branches just mentioned. Immediately beyond this the two lateralis nerves meet and fuse, the lateralis X reaching the other through a canal which it enters after leaving the main vagus trunk. Immediately beyond the point of fusion another laterally trending twig is given off from the combined nerve.

The subsequent course of the combined lateralis VII–X is caudad, parallel and deep to the lateral line canal; at least it is so assumed; the nerves were not traced beyond the commencement of the fleshy wall of the branchial chamber.

The sensori-motor division of the nervus facialis has no communication with the fifth nerve other than through the inferior mandibular nerve to be described later. Its root enters a canal in front of the otic capsule and there lies the geniculate ganglion, completely separated by cartilage from both the gasserian and lateralis ganglia. The ramus palatinus leaves the ganglion in a ventral direction; lying still within its own canal the nerve bends forward around the posterior wall of the canal for the internal cerebral artery and then continues forward enclosed in the cartilage until the posterior margin of the pterygopalatine bone is reached. The nerve now turns more markedly laterally and emerges from beneath the bone at the transverse level of the teeth. The vidian canal is provided with a floor by the pterygopalatine bone, but is lodged in cartilage above the parasphenoid bone.

The hyomandibular division of the nerve runs laterally and caudally through the hyomandibular canal between the very much enlarged otic and the basal process of the quadrate and emerges above the short vertical posterior margin of the quadrate deep to the antero-dorsal corner of the operculum. Here it divides into several branches. The first of these penetrates a foramen, in the posterior margin of the otic process, which lies immediately superficial to the external aperture of the hyomandibular canal. This is a sensory branch which apparently communicates with the first of the laterally trending branches of the lateralis nerve whose canal terminates just anteriorly to this foramen, but the tissues here are exceedingly tough and permeated by bony spicules, related to the lateral line canal, which make dissection very difficult. The second branch is the inferior mandibular nerve already mentioned. This runs ventrad along the posterior margin of the quadrate for a short distance and then turns forward through a canal in the quadrate cartilage close to the surface and not far above the articular head. This canal opens anteriorly about half-way across the quadrate body, and from here the nerve runs forward on the surface of the cartilage and under cover of the lower edge of those fibres of the M. quadratomandibularis which here take origin directly from the cartilage. Turning ventrad just a little further forward, in the tissues of the cheek just behind the angle of the mouth, the nerve enters the myloid canal as already described.

The third branch of the nerve runs parallel to the inferior mandibular but continues on in the same direction after that turns forward. This nerve thus comes to reach the tissues overlying the posterior end of the lower jaw. Here it turns forward and breaks up into twigs distributed to the subcutaneous tissues behind and superficial to the posterior part of the Csv. 1. muscle. No twigs could be traced to that muscle.

The remaining branches of the hyomandibular division of the facial nerve are the motor twigs to the Mm. levator operculi, interhyoideus and Cs. 2. They are distributed over the surface of these muscles and many of their twigs, very definitely, terminate in the muscles; others of the twigs, however, do not so terminate, and these are probably cutaneous sensory fibres.

The Auditory Nerve.

The eighth nerve arises by two vestibular roots and four labryinthine. All arise close together ventral to and just behind the sensori-motor root of the facial nerve, from the side wall of the medulla close to the inferior margin. The vestibular roots are between the labyrinthine and the facial root.

The two vestibular roots pass directly to the vestibule, side by side, and break up into numerous fine terminal twigs on its medial wall. In similar manner the labyrinthine roots proceed to the medial wall of the otolith chamber and end in a "fan" of strands each of which divides again into fine twigs distributed over the wall of the chamber.

The Glossopharyngeal Nerve.

The ninth nerve arises by a single root from the side of the medulla. Its point of origin is ventral to the vagus roots and a short distance in front of the most anterior of them. Bing and Burckhardt (1905) represent the roots of these two nerves and those of the fifth, seventh and eighth nerves very much more crowded together than has been the condition in any of the four specimens which have been available for the present investigation.

No trace of any communication between this and the vagus nerve was seen.

The root is remarkably long, resembling that of *Scaphyrhynchus* as described by Norris (1925). It runs caudally and laterally along the dorso-lateral margin of the vagus roots until it has passed the otic capsule; it then turns laterally and enters a canal which runs around the posterior and ventro-lateral wall of that cavity and opens on the ventrum of the skull posteriorly to the basal root of the quadrate. The glossopharyngeal ganglion lies in this canal towards its external aperture. Leaving the ganglion, the nerve divides into palatine and branchial divisions. The palatine division runs forward along the lateral margin of the parasphenoid bone. Where the two bones make contact at this margin the nerve passes on to the ventral surface of the pterygo-

palatine bone. As it runs forward across this bone it gives off a number of small twigs and terminates in the thick mucosa just behind the palatine teeth.

The branchial division was not dissected out.

The Vagus Nerve.

The tenth nerve arises by several roots from the side of the medulla dorsally to both the pyramidal and lateral columns. There are the usual two main divisions of the roots. The anterior lateralis is a single stout collection of fibres which arises directly dorsally to the root of the ninth nerve. The posterior division is composed of four groups of strands, the first of which arises a short distance behind the anterior division at the same level, and the other three in the same line, each in contact with that in front of it. Gathered together into one rounded bundle these enter the vagus foramen and at once enter the vagus ganglion. This ganglion is imperfectly divided into two portions. The depth of the vagus foramen communicates with two wide canals, that for the lateralis trunk and that for the remainder of the nerve. The ganglion extends into both canals and there is quite a marked increase in the girth of the lateralis portion just within its canal. The lateralis canal turns laterally; it is relatively short and ends in the posterior end of the lateralis VII canal. Beyond the branches already mentioned the ramifications and course of the lateralis X were not investigated.

The ramus gastro-intestinalis was only followed as far as the posterior end of the branchial chamber. The ganglion is very large and extrudes through the posterior aperture of the canal, and one small and three large branchial nerves arise directly from the extruded portion. These are spread out slightly so as to have the appearance of arising from the ventral side of the thickened base of the main nerve.

The Occipital Nerve.

This eleventh nerve is a typical spinal nerve. It arises by single dorsal and ventral roots which leave the cranial cavity by their own canals, join in a ganglion, which lies in the cartilage and then divide into dorsal and ventral nerves. The origin of the roots is in line with those of the rest of the spinal nerves.

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